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ECONOMIC SUBSTITUTABILITY OF ELECTRICAL BRAIN STIMULATION, FOOD, AND WATER

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Concurrent variable-ratio schedules of electrical brain stimulation, food, and water were paired in various combinations as reinforcement of rats' lever presses. Relative prices of the concurrent reinforcers were varied by changing the ratio of the response requirements on the two levers. Economic substitutability, measured by the sensitivity of response ratio to changes in relative price, was highest with brain stimulation reinforcement of presses on both levers and lowest with food reinforcement of presses on one lever and water reinforcement of presses on the other. Substitutability with brain stimulation reinforcement of presses on one lever and either food or water reinforcement for presses on the other was about as high as with brain stimulation for presses on both levers. Electrical brain stimulation for rats may thus serve as an economic substitute for two reinforcers, neither of which is substitutable for the other.

Key words: substitutability, economics, concurrent variable-ratio schedules, electrical brain stimulation, food, water, lever press, rats

Since its discovery (Olds & Milner, 1954), the reinforcing effect of electrical stimulation of the brain (EBS) has been studied extensively, and a number of theories have been proposed to account for its action. Some theories treat EBS as a unique reinforcer, some propose a common mechanism for EBS and other specific reinforcers (e.g., food, cocaine), and others consider EBS to activate a neural substrate common to all reinforcers. (See, e.g., Hoebel & Teitelbaum, 1962; Olds, 1958; Spies, 1965; see Mogenson & Cioé, 1977, for comparisons between EBS and conventional reinforcers and for discussion of the mechanisms of EBS reinforcement.)

The present experiment ignores the question of internal mechanism and takes a behavioral approach to EBS reinforcement in rats. We ask, to what extent is EBS economically substitutable for food and water, two reinforcers that are known to be relatively nonsubstitutable for each other by rats (Rachlin, Green, Kagel, & Battalio, 1976). A finding that EBS is highly substitutable for both food and water would mean that EBS is a general reinforcer (at least with respect to eating and drinking) regardless of how the underlying physiological mechanism might work. A finding that EBS is highly substitutable for food but not for water would imply that EBS functions like food reinforcement. A finding that EBS is substitutable for neither food nor water would indicate that EBS is an independent reinforcer relative to the other two.

Previous behavioral studies of EBS have examined the strength of EBS as a reinforcer relative to food or to leisure (the inverse of responding) (e.g., Hawkins & Pliskoff, 1964; Sidman, Brady, Boren, Conrad, & Schulman, 1955) or the effects of varying brain-stimulation parameters on responding for EBS in choice situations (e.g., Davis, Davison, & Webster, 1972; Fray, 1981; Hodos & Valenstein, 1962) but have not examined substitutability as such. One study specifically directed to the question of economic equivalence for rats of EBS and food (Hursh & Natelson, 1981) used concurrent variable-interval (VI) schedules of food and EBS in a closed economy and found the two reinforcers to be nonequivalent in demand elasticity; as the VI value of both concurrent schedules increased, EBS rate decreased while food consumption remained about constant. However, the procedure used in the Hursh and Natelson study does not allow direct assessment of substitutability. Both

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of the VI schedules were changed together in the same direction (e.g., from concurrent VI 60 s 60 s in one condition to concurrent VI 15 s VI 15 s in another) and no provision was made for income compensation, because the subjects were permitted to work around the clock.

Another experiment, by Hollard and Davison (1971), provides incidental evidence regarding substitutability between EBS and food with pigeons as subjects. Using several pairs of concurrent VI schedules, pigeons matched time allocation ratio to the ratio of EBS versus food reinforcement. The slope of the matching function (on log–log coordinates) was close to 1.0. Rachlin, Kagel, and Battalio (1980) have shown that a unit slope of such a function will be obtained only if the alternatives are completely substitutable. Thus, for pigeons, EBS is substitutable for food. It is unlikely, however, that this result can be generalized to rats. Miller (1976) found complete substitutability between different grains for pigeons, but various foods have not been found to be completely substitutable for each other by rats.

Figure 1 shows the technique used to measure substitutability in the present experiment. Line 1 is the budget constraint determined by concurrent variable-ratio (VR) schedules. The filled circle on Line 1 is a hypothetical obtained consumption pattern. Line 2, drawn through the filled circle, represents another pair of concurrent VR schedules. In economic terms, Line 2 represents an "income-compensated price change" from Line 1; a subject under the new schedules (Line 2) could still obtain the identical amounts of the two reinforcers that it did under the previous schedules (Line 1). Any change in consumption pattern from Line 1 to Line 2 must be due to the difference in the slopes of the two lines (which, in turn, represents the relative price of the two commodities). The degree to which a subject's response allocation shifts in the direction of the arrow (as shown by a series of open circles) represents (ordinally) the degree of substitutability of the two reinforcers for that subject (see Rachlin, 1989, Chapter 8, for a more detailed explanation). In Figure 1, Budget Constraint 2 represents an increase in the price of Reinforcer Y relative to Reinforcer X. With the assumption of a specific form of utility function, this procedure can yield a (ratio-scale) measure of the degree of substitutability between reinforcers (Rachlin et al., 1976).

METHOD

Subjects

Female albino rats were housed in individual cages. The colony room was maintained on a 12:12 hr light/dark cycle. During conditions in which food and/or water served as the reinforcer, the rats were given 30-min access to the respective substance(s) 45 min after the daily session; during conditions in which food and/or water did not serve as a reinforcer, the rats had free access to the respective substance(s) in their home cages (e.g., when the reinforcers were EBS and water, the rats had free access to food in their home cages and were permitted 30-min access to water after each session).

Stainless steel bipolar electrodes (Plastic Products) were stereotaxically implanted under sodium pentobarbital anesthesia. Coordinates for lateral hypothalamus were taken relative to Bregma and were posterior 0.2 mm, lateral 1.5 mm, and down 8.0 mm from the skull.

Upon completion of testing, the implanted rats were sacrificed by overdose of sodium pentobarbital and perfused with saline and 10% formalin. Frozen brain sections were cut at 40 μm and stained with cresyl violet. Examination of the sections revealed electrode tracts terminating near or just medial to the lateral hypothalamic nucleus.

Apparatus

A Gerbrands two-lever test chamber measured 33.6 cm long by 29.8 cm wide by 31 cm high. The chamber was enclosed in a light- and sound-attenuating box with a ventilation fan and white noise generator. A 6-W white light located at the top of the chamber provided general illumination.

The stainless steel levers were 5.1 cm wide and were located approximately 10 cm from the grid floor and 3.5 cm from each side wall. A force of at least 0.39 N was required to operate the lever and produce an audible feedback click.

Presses on the left lever could cause delivery of electrical brain stimulation or food pellets. Each food reinforcer consisted of four 45-mg

Noyes food pellets. Presses on the right lever could cause delivery of EBS or water. Each water reinforcer was 2.4-s access to a 0.1-cc dipper cup. Food and water were accessible through an opening (4.5 cm by 6.5 cm) located 2.0 cm below each lever. During reinforcement, the chamber light was extinguished and a 6-W white light behind and above the opening was illuminated for 2.4 s.

EBS was administered via a connecting cable from a 60-cycle stimulator through a mercury commutator on the roof of the chamber. EBS reinforcement consisted of four pulses, each 0.15 s long and timed 0.2 s apart, with a current of 50 μA. During food–EBS conditions, responding on the left lever produced food and responding on the right lever produced EBS; during water–EBS conditions, responding on the left lever produced EBS and responding on the right lever produced water. During EBS, the chamber light was extinguished and a 6-W white light located 9.5 cm over the appropriate lever flashed coincident with each pulse of stimulation.

Procedure

Subjects A, B, and C were initially shaped to lever press for EBS on a continuous schedule of reinforcement. Once pressing was reliable, the schedule was gradually increased to a variable ratio of 15 presses. All subjects were then shaped to press for food and water in a similar manner.

During each of the conditions of this experiment, the rats were placed in the experimental chamber every day for a session that terminated when the sum of the responses on the two levers equaled a total, T, which varied across conditions. Reinforcement was programmed on each lever according to VR schedules, VR_x and VR_y. The parameters T, VR_x, and VR_y are the independent variables of this experiment; they constitute the rats' "budget." Lines 1 and 2 in Figure 1 represent different budgets. The dependent variable of this experiment is the rats' allocation of responses to the levers. A rat could allocate its T responses between the two levers in any proportion. A rat that allocated all of its responses to the VR_x lever would receive, on average, a number of X reinforcers equal to T/VR_x and no Y reinforcers. Such an allocation would be represented in Figure 1 by the point of intersection of the budget line with the x axis. Correspondingly, an allocation of all T responses to the VR_y lever would be represented by the point of intersection of the budget line with the y axis. A rat that allocated x responses to the VR_x lever and y $(= T - x)$ to the VR_y lever would receive a number of X reinforcers and Y reinforcers equal to x/VR_x and y/VR_y, respectively. The filled and unfilled points on the lines in Figure 1 represent several nonexclusive allocations of responses to the two levers. The various conditions of this experiment may thus be specified in terms of three parameters, VR_x, VR_y, and T, together with the specification of kind and amount of each delivery of Reinforcer X and Reinforcer Y.

There were three kinds of reinforcement in this experiment: food (F), water (W), and electrical brain stimulation (EBS). Table 1 identifies the conditions in sequence for each rat. Each condition lasted a minimum of 14 days

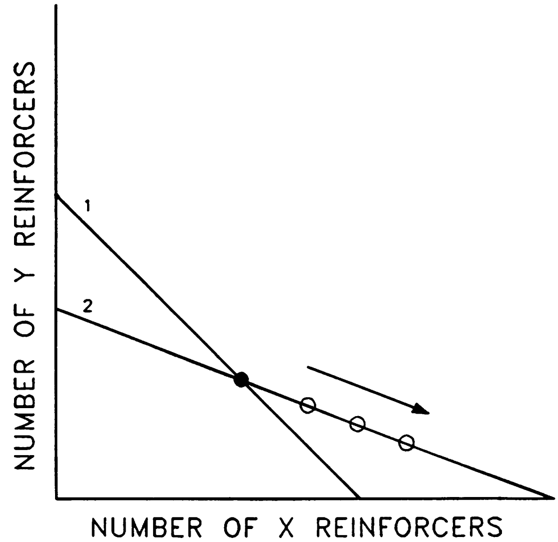

Fig. 1. Experimental procedure. Line 1 is the budget constraint imposed by concurrent VRVR schedules, and the filled circle represents a hypothetical obtained consumption pattern. Line 2 represents another pair of concurrent VRVR schedules in which the price (VR value) of Reinforcer Y has been increased and the price (VR value) of Reinforcer X has been decreased. This budget constraint (Line 2) is selected so that it runs through the filled circle. Thus, the subject could obtain amounts of both reinforcers identical to those obtained under the previous schedules (Line 1). The degree of substitutability of the two reinforcers is indicated by the degree to which response allocation shifts in the direction of the arrow.

Table 1

Sequence of conditions.

Subject	Condition	Kind of reinforcer X	Kind of reinforcer Y	Total responses ($T = x + y$)	Programmed schedule VR_x	Programmed schedule VR_y	Number of sessions
A	1	EBS	F	900	15	15	23
	2	EBS	F	1,583	30	7.5	30
	3	EBS	F	764	7.5	30	14
	4	EBS	W	900	15	15	18
	5	EBS	W	1,529	30	7.5	22
	6	EBS	W	714	7.5	30	16
	7	EBS	W	1,979	40	5	27
	8	W	F	900	15	15	20
	9	W	F	1,667	7.5	30	14
	10	W	F	2,194	5	40	14
	11	EBS	EBS	1,800	30	30	14
	12	EBS	EBS	900	15	15	14
	13	EBS	EBS	1,361	7.5	30	14
B	1	EBS	EBS	900	15	15	18
	2	EBS	EBS	1,227	30	7.5	16
	3	EBS	EBS	1,027	7.5	30	14
	4	EBS	EBS	1,800	30	30	18
	5	EBS	F	900	15	15	32
	6	EBS	F	1,258	30	7.5	20
	7	W	F	900	15	15	104
	8	W	F	1,245	7.5	30	23
	9	W	F	1,032	30	7.5	82
	10	W	F	1,532	5	40	24
C	1	EBS	F	900	15	15	23
	2	EBS	F	1,794	30	7.5	28
	3	EBS	F	1,208	20	10	14
	4	EBS	F	1,220	20	15	22
	5	EBS	W	900	15	15	14
	6	EBS	W	1,772	30	7.5	26
	7	EBS	W	1,191	20	10	15
	8	W	—	1,200	10	—	19
	9	W	F	900	15	15	17
	10	W	F	1,346	7.5	30	20
	11	W	F	896	30	7.5	22
	12	W	F	1,553	15	15	20
	13	W	F	2,981	7.5	30	14
	14	W	F	1,491	7.5	30	22
D	1	W	F	900	15	15	20
	2	W	F	1,733	7.5	30	18
	3	W	F	599	30	7.5	58
	4	W	F	2,282	5	40	26
E	1	W	F	900	15	15	31
	2	W	F	1,275	7.5	30	25
	3	W	F	971	30	7.5	103
	4	W	F	1,584	5	40	25

and was changed when relative responding was judged stable (as determined from visual inspection of the data from the last 10 days).

For each pair of reinforcers (except for Condition 11 with Rat A), the initial budget parameters were always $VR_x = 15$, $VR_y = 15$, $T = 900$. Parameters of subsequent conditions depended on the results with the initial conditions and were changed in two ways: (a) The VR values were changed to give the budget line a different slope, and (b) T was adjusted so that the new budget line crossed the initial one at the point representing the subject's initial allocation (as illustrated in Figure 1).

In addition to the three main comparisons of this experiment (F vs. EBS, W vs. EBS, F vs. W), a control condition exposed 2 of the rats to EBS reinforcement of presses to both levers (EBS vs. EBS). With concurrent VR food reinforcement (F vs. F), pigeons allocate key pecks almost exclusively to the key with the lower VR requirement (Green, Rachlin, & Hanson, 1983; Herrnstein & Loveland, 1975). Behavioral economic theory (Rachlin, 1978) explains such exclusive allocation in terms in maximization of the rate of (completely substitutable) reinforcement. Food reinforcement for food-deprived pigeons evidently overwhelms any tendency to alternate (which predominates only when the alternative VR schedules are exactly equal). Alternation with concurrent ratio schedules of identical reinforcers may be viewed as residual nonsubstitutability, perhaps due to the different key colors or to different muscular movements involved in pecking on the different keys. The EBS vs. EBS control conditions were investigated to determine whether EBS reinforcement acts like food reinforcement in this respect and also to provide a baseline of maximum substitutability (of EBS for itself) against which substitutabilities of EBS for food and for water might be measured.

Other conditions will be described as they are presented and discussed.

RESULTS

Table 2 shows the results averaged over the last 10 sessions of each condition for each rat. The duration of the sessions varied considerably and generally was related to T, the total number of responses. Because the ratio schedules were variable, the obtained number of responses per reinforcer (p and q) differed slightly from that programmed (VR_x and VR_y). In all subsequent calculations, we use the actual (obtained) ratio values (p and q) rather than the nominal (programmed) ones (VR_x and VR_y).

Let us consider first the two extreme cases: EBS vs. EBS, in which substitutability is expected to be maximal, and F vs. W, in which, on the basis of previous experiments, substitutability is expected to be minimal. Figure 2 shows these comparisons for the 3 implanted rats. (The electrode of Rat C broke before the EBS vs. EBS condition could be studied.)

The budget lines of Figure 2 were determined by dividing total responses, T, by VR_x (to obtain the x intercept) and by VR_y (to obtain the y intercept). Each allocation point (the filled circle) was located on or near its budget line by using the mean number of reinforcers obtained (X and Y) from the last 10 sessions. The closeness of the points to the programmed budget lines indicates that the VR schedules obtained (p and q) did not differ appreciably from those programmed (VR_x and VR_y).

As with pigeons exposed to equal VR schedules of food reinforcement for pecking keys, the rats in this experiment exposed to equal VR schedules of EBS reinforcement showed no clear preference. However, when the VR schedules were unequal, both rats showed very strong preferences for the lower ratio lever (averaging 97% of responses on the lower ratio lever).

The open circles in Figure 2 are replications with both VR values and total responses, T, doubled ($VR_x = 30$, $VR_y = 30$, $T = 1{,}800$). In economic demand theory, a doubling of income and price together constitutes no change in real price. Of course, in these experiments, as in real-world economies, behavior might change when prices and income are raised proportionally, because the subjects must work longer for the same income and forfeit some amount of leisure. Therefore, in order to check that allocation does not significantly change, we studied this control condition; behavior was little affected (see also Allison, Miller, & Wozny, 1979). Moreover, the fact that the rats responded throughout the concurrent VR 30 VR 30 schedule with $T = 1{,}800$ also demonstrates that they can complete such relatively high ratio values for EBS reinforcement.

The results with food and water (see Figure 2, lower figures) confirm previous results (Rachlin et al., 1976) in that the shift of consumption with shift of relative price (slope of budget line) is much less extreme than with highly substitutable reinforcers.

Rat C was exposed to several additional F vs. W comparisons. In Condition 12, concurrent VR 15 VR 15 schedules were used but with the budget line passing through the point obtained under Condition 11. This budget line is thus parallel to the baseline (Condition 9). In Condition 13, the change in slope now produces a budget line parallel to that of Condition 10. These conditions were conducted to demonstrate that the results obtained were not somehow dependent on the initial value of $T = 900$.

Condition 14, like Condition 13, used con-

Table 2

Results (means of last 10 sessions of each condition).

Condition		Session duration (min)	Obtained					
			Responses		Reinforcers		VR	
			x	y	X	Y	($p = x/X$)	($q = y/Y$)
A	1	10.46	709.0	192.3	49.5	13.1	14.3	14.7
	2	58.21	462.0	1,121.1	14.7	149.1	31.4	7.5
	3	8.04	746.1	17.8	99.5	0.5	7.5	35.6
	4	13.01	721.1	178.9	48.0	11.8	15.0	15.2
	5	21.26	976.5	552.5	32.3	74.3	30.2	7.4
	6	8.13	711.8	2.2	95.2	0	7.5	[30]
	7	80.06	1,076.5	903.4	27.3	181.4	39.4	5.0
	8	30.97	89.7	810.3	5.9	54.1	15.2	15.0
	9	33.91	223.1	1,442.8	29.5	48.1	7.6	30.0
	10	44.29	290.4	1,903.3	57.3	47.8	5.1	39.8
	11	59.33	333.3	1,466.7	11.0	48.9	30.3	30.0
	12	16.11	292.5	607.5	19.5	40.5	15.0	15.0
	13	27.41	1,304.5	56.5	173.5	1.5	7.5	37.7
B	1	39.22	515.2	384.8	34.5	25.6	14.9	15.0
	2	40.86	28.2	1,198.8	0.9	159.7	31.3	7.5
	3	31.34	1,007.3	19.7	134.3	0.6	7.5	32.8
	4	233.54	1,157.6	642.4	38.7	21.5	29.9	29.9
	5	18.72	513.4	386.7	35.4	26.1	14.5	14.8
	6	117.03	77.0	1,188.8	3.2	148.2	24.1	8.0
	7	25.69	372.2	528.0	25.6	35.1	14.5	15.0
	8	23.12	277.1	968.2	37.5	31.7	7.4	30.5
	9	43.49	609.2	422.8	20.4	55.9	29.9	7.6
	10	25.29	241.2	1,290.6	48.1	31.2	5.0	41.4
C	1	15.05	869.7	30.0	59.2	2.4	14.7	12.5
	2	84.75	175.8	1,618.2	5.8	215.6	30.3	7.5
	3	40.21	57.5	1,150.5	3.2	114.4	18.0	10.1
	4	22.88	1,113.8	106.1	55.8	6.9	20.0	15.4
	5	24.17	869.3	30.7	58.6	1.9	14.8	16.2
	6	47.86	759.1	1,012.9	25.3	135.7	30.0	7.5
	7	30.13	746.7	444.1	37.5	44.3	19.9	10.0
	8	86.97	1,200.0	—	120.0	—	10.0	—
	9	19.04	305.4	594.6	19.9	39.9	15.3	14.9
	10	21.85	396.5	949.2	53.0	31.8	7.5	29.8
	11	31.12	160.9	735.1	5.5	98.0	29.3	7.5
	12	36.06	634.0	919.0	42.7	61.5	14.8	14.9
	13	92.01	964.7	2,015.9	128.8	67.1	7.5	30.0
	14	64.03	1,133.6	1,847.6	151.4	62.9	7.5	29.4
D	1	33.84	80.5	819.5	5.9	56.3	13.6	14.6
	2	38.40	392.3	1,344.8	50.7	44.0	7.7	30.6
	3	32.66	13.5	585.5	0.4	77.3	33.8	7.6
	4	42.95	319.0	1,963.1	62.8	48.1	5.1	40.8
E	1	30.04	355.9	544.0	23.2	36.7	15.3	14.8
	2	26.97	372.1	903.1	49.8	27.3	7.5	33.1
	3	36.48	591.4	379.6	22.2	51.0	26.6	7.4
	4	27.66	260.9	1,323.2	50.8	33.0	5.1	40.1

current VR 30 VR 7.5. However, each daily session ended after half as many responses (1,491 instead of 2,981). This condition tested whether results were constrained by the number of responses required or reinforcers obtained. The results from this condition (shown as an open square in Figure 2) are based on 2-day sums so as to be comparable to Condition 13.

Finally, Condition 8 was a water-only condition. Here, responses on the right lever still produced water, and responses on the left had no effect. Under the VR 10 with T = 1,200, Rat C completed the condition in under 1.5

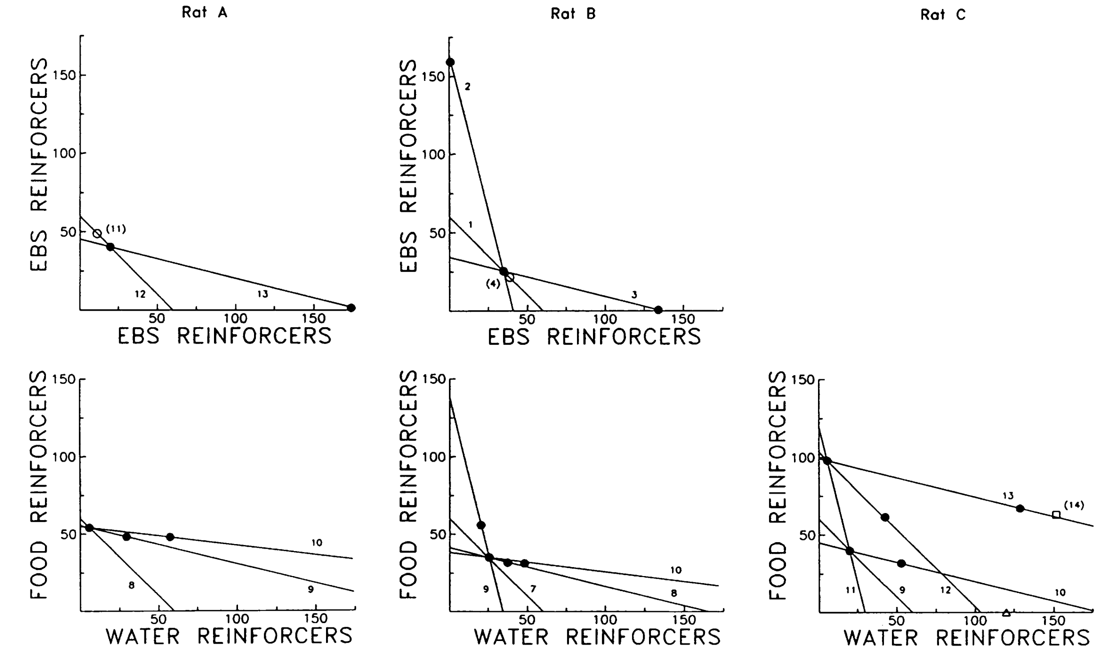

Fig. 2. Amounts of reinforcers consumed. Filled circles and open symbols represent results from experimental and control conditions, respectively. The upper figures present the results from conditions in which the rats chose between EBS reinforcement from the left and right levers. The lower figures present the results from conditions in which presses on the left lever led to food and presses on the right lever led to water reinforcement. Numbers indicate the budget lines of the different conditions; numbers in parentheses refer to control conditions (see Table 1).

hr and received 120 water reinforcers (the open triangle in Figure 2). This result, along with that from Condition 14, demonstrates that the rat can consume such large amounts of water during the session and that the relative non-substitutability between water and food was not somehow artificially induced by the amount of water or food. In general, these control conditions indicate that behavior in the F vs. W conditions was sensitive to the budget constraints.

Two additional (unimplanted) rats were also exposed to the F vs. W conditions: Both rats (data not shown in Figure 2, but see Tables 1 and 2, Rats D and E) showed patterns of choice much like the others.

Figure 3 shows budget lines and allocation points for each of the 3 rats with F vs. EBS (upper figures) and W vs. EBS (lower figures). (Rat B was not exposed to the water vs. EBS condition because its electrode broke.) Casual inspection indicates that, under initial conditions ($VR_x = 15$, $VR_y = 15$, $T = 900$), all 3 rats preferred EBS reinforcement to food reinforcement, and both rats exposed to EBS vs. W preferred EBS reinforcement to water reinforcement. These initial preferences confirm previous results that with balanced schedules (relatively low and equal prices) EBS is generally preferred to food and water (e.g., Falk, 1961; Hursh & Natelson, 1981; Spies, 1965). However, when EBS was made more expensive, preferences of all rats shifted inversely. Rats may prefer food or water to EBS or vice versa, depending on relative price. It appears from the degree of shift of the rats' preferences in response to shifts of relative price that EBS is highly substitutable for food (almost as much as EBS is substitutable for itself) but somewhat less highly substitutable for water. Nevertheless, EBS seems to be much more substitutable for water than food is for water.

These general observations can be quantified if the rats' changes in allocation are assumed to maximize utility, where utility is a function of consumption of both reinforcers.

Calculation of Substitutability

The concurrent ratio schedules (p and q) and the total number of responses that ended

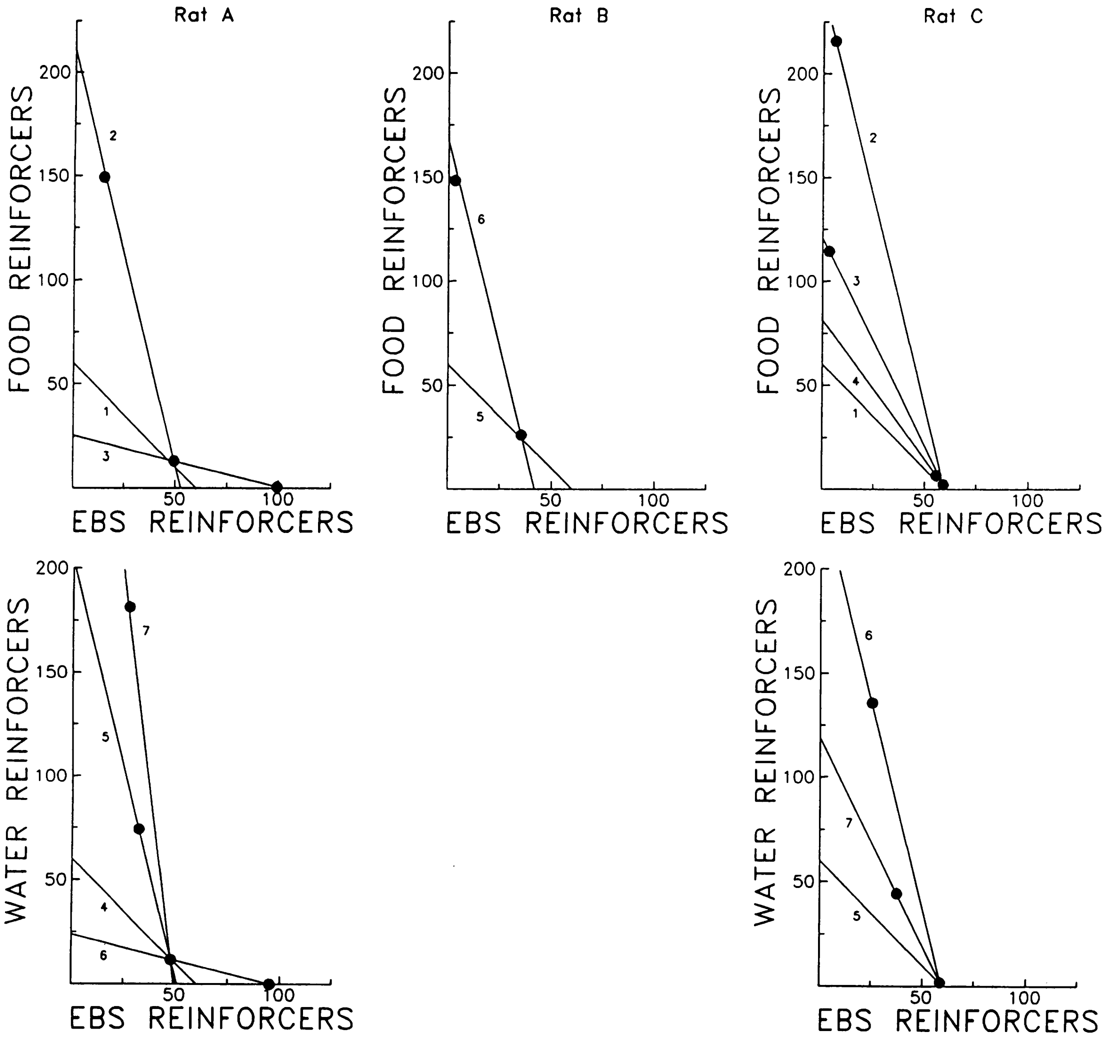

Fig. 3. Amounts of reinforcement consumed. The upper figures present the results from conditions in which presses on the left lever led to food and presses on the right lever led to EBS reinforcement. The lower figures present the results from conditions in which presses on the right lever led to water and presses on the left lever led to EBS reinforcement. Numbers indicate the budget lines of the experimental conditions (see Table 1).

the session ($T = x + y$) constrain the number of reinforcers obtained (X and Y) as follows:

$$pX + qY = T. \quad (1)$$

Equation 1 is the equation of the budget lines drawn in Figures 2 and 3.

Equation 2 is a form of utility function, maximization of which has successfully described rats' choices between food and water (Rachlin et al., 1976), between food and leisure (Schrader & Green, 1990), between food pellets and food-sugar pellets (Baum, 1990), and pigeons' choices between food and leisure (Green, Kagel, & Battalio, 1982, 1987):

$$U = aX^s + bY^s \quad (2)$$

where U is utility, a and b are constants representing the utility of a single Reinforcer X or Reinforcer Y, X and Y are numbers of Reinforcer X and Reinforcer Y, and s is a constant representing degree of substitutability between Reinforcer X and Reinforcer Y. Normally, $0 < s < 1$. However, s takes on negative values when reinforcers are complements rather than substitutes. In economics, two reinforcers (commodities) are said to be complements when greater amounts of one increase demand for the other. (Left shoes and right shoes or bicycle frames and bicycle wheels are complements.) Food and water occasionally have been found to be complements for hungry and thirsty animals (Hursh, 1978; Hursh & Bauman, 1987; Kagel, Battalio, Green, & Rachlin, 1980). When $s = 0$, reinforcers are said to be independent (neither complements nor substitutes).

As $s \to 1$, Reinforcer X and Reinforcer Y approach complete substitutability; straight-line indifference contours (loci of points among which subjects are indifferent) drawn on Figures 1, 2, and 3 would represent complete substitutability. Lesser degrees of substitutability (lesser positive values of s) would be represented in Figures 1, 2, and 3 by curved indifference contours convex to the origin. With curved contours, the more of each reinforcer obtained, the less that reinforcer would be worth relative to the other (the economic law of diminishing marginal utility).

Maximizing utility (Equation 2) given the constraints on obtained reinforcers (Equation 1) implies[1]:

$$\mathrm{X}/\mathrm{Y} = k(q/p)^n, \tag{3}$$

where $k = (a/b)^n$ and $n = (1 - s)^{-1}$. Equation 3 says that with concurrent ratio schedules, subjects that maximize utility (where utility is given by Equation 2) will match the ratio of obtained reinforcers (X/Y) to a power function of the inverse of the obtained ratio-schedule values (q/p). Note that as $s \to 1$ (complete substitutability), $n \to \infty$, and Equation 3 predicts complete allocation to whichever alternative corresponds to the lower ratio, as is typically found (Green et al., 1983; Herrnstein & Loveland, 1975).

Substituting the dependent variable, x/y (the subjects' allocation of responses to the two levers) for the obtained reinforcer ratio, X/Y (where $\mathrm{X} = x/p$ and $\mathrm{Y} = y/q$), a function may be derived relating the dependent variable (relative allocation) to the independent variable (relative price):

$$x/y = k(q/p)^m \tag{4}$$

where $m = n - 1 = s/(1 - s)$.

Table 3

Substitutabilities.

	Rat A	Rat B	Rat C	Rat D[a]	Rat E[a]
EBS vs. EBS	0.72	0.73	—	—	—
F vs. EBS	0.61	0.73	0.81	—	—
W vs. EBS	0.61	—	0.71	—	—
F vs. W	0.14	−1.5	0.17	0.39	−1.3

[a] Unimplanted rats; data not shown in Figures 2 and 3.

Table 3 shows the substitutability (s) between each pair of reinforcers for each rat tested. The substitutabilities were obtained by a linear regression between the natural log of the inverse of the relative price, $\ln(q/p)$, and the natural log of the relative allocation, $\ln(x/y)$. The slope of the regression equation is the exponent, m, of Equation 4. Then, $s = m/(1 + m)$. There were not enough budget conditions in this experiment to test Equation 2 vis à vis other conceivable utility functions. Equation 2 was used here merely to provide a convenient metric for substitutability. Nevertheless, generally high coefficients of correlation (median r^2 between $\ln(x/y)$ and $\ln(q/p)$ was .938) indicate that Equation 2 was at least not inappropriate for this purpose.

DISCUSSION

From Table 3 it is clear that EBS was fairly highly substitutable for itself with the two rats tested under this condition ($s = 0.72$ and 0.73). But there were limits to that substitutability ($s < 1$). These limits may be due to a tendency to alternate, which ensures that, however advantageous one alternative may be, other alternatives are occasionally sampled. In the context of the experiment as a whole, alternatives did change in value periodically; previously low-valued alternatives could, on occasion, suddenly become highly valuable. A tendency to sample all alternatives occasionally, in this context, would be highly adaptive. However, the changeableness of value of various alternatives is a characteristic of rats' natural environments as well as of the present experi-

[1] $(dU/d\mathrm{Y}) = -(saq/p)[T - q\mathrm{Y})/p]^{(s-1)} + sb(\mathrm{Y})^{(s-1)}$
$= -(saq/p)(\mathrm{X})^{s-1} + sb(\mathrm{Y})^{s-1} = 0$

$$\mathrm{Y}/\mathrm{X} = (a/b)^{(1/(s-1))}(q/p)^{(1/(s-1))}$$

$$\mathrm{X}/\mathrm{Y} = (a/b)^{(1/(1-s))}(q/p)^{(1/(1-s)}$$

ment; therefore, there is no way to tell to what extent the tendency to sample low-valued alternatives was a response to the overall contingencies of the present experiment and to what extent it is an innate characteristic of the behavior of rats (for further discussion, see Krebs, Kacelnik, & Taylor, 1978; Olton, 1982).

At the other extreme, food and water were either barely substitutable (Rats A, C, and D) or complementary (Rats B and E). This result replicates previous findings (Rachlin et al., 1976). The negative values of s shown by Rats B and E are examples of antimatching. Substituting the usual variables of the matching equation for the variables in Equations 3 and 4:

$$x/y = k^{1-s}(X/Y)^{s}. \qquad (5)$$

Equation 5 is a form of the generalized matching equation (Baum, 1974), which relates the ratio of responses (x/y) to the ratio of reinforcements (X/Y). Complementarity ($s < 0$) implies antimatching (Rachlin, Battalio, Kagel, & Green, 1981); relative rate of response varies *inversely* with relative rate of reinforcement. Although antimatching may be explainable by melioration theory (Herrnstein & Vaughan, 1980) in terms of varying response structure and differing satiation rates for food and water, this finding follows in a straightforward way from the present account of choice in terms of maximization.

Table 3 also makes it clear that, given our approach to its determination, the substitutability of EBS for food and for water is (a) about equal and (b) almost as great as the substitutability of EBS for itself. The physiology underlying a rat's demand for food or water is undoubtedly highly complicated, involving mechanisms at peripheral, medial, and central levels. Interaction of two such systems must be still more complicated. The present results say nothing about whether EBS involves a general "pleasure center" in the brain. It is conceivable, for instance, that EBS, with the parameters used in the present experiment, stimulates differing central mechanisms responsible for both food reinforcement and water reinforcement. Additionally, the complementarity between the two systems as studied here could be at the peripheral level; food dries the mouth. However, the present results do indicate that, as an economic good, EBS (like money in a human economy) is highly substitutable for at least two reinforcers that are not substitutable for each other.

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